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Effects of N addition and precipitation reduction on soil respiration and its components in a temperate forest

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ABSTRACT

As the important pathway for soil carbon (C) fluxes from terrestrial ecosystems to the atmosphere, soil respiration (*Rs*) is strongly regulated by soil nitrogen (N) and water availability. Knowledge of the effect of soil N and moisture availability on *Rs* and its components (heterotrophic respiration (*Rh*) and autotrophic respiration (*Ra*)) is important understand soil C responses to climate change. Therefore, an 8-year field manipulation experiment to investigate the responses of *Rs* and its components to a reduction in the growing season precipitation amount with or without N addition was conducted in northern China. The results show that the average annual *Rs*, *Rh*, and *Ra* rates increased on average by 47%, 94%, and 38%, respectively, under the N addition treatments; increased on average by 18%, 53%, and 24%, respectively, under the precipitation reduction treatments; and increased on average by 5%, 4%, and 6%, respectively, under their interaction. The *Rs* and *Rh* were positively correlated with fine root biomass and microbial biomass, whereas the *Ra* was only related to the fine root biomass. Nitrogen addition and precipitation reduction significantly increased the *Rs*, *Rh* and *Ra*, possibly due to increased root biomass and microbial biomass. The *Rs* and *Rh* were not significantly affected by the interaction of N addition and precipitation reduction, whereas their combined effects significantly decreased the *Ra*. The *Rs* and *Ra* were also negatively correlated with soil total P concentration. The N addition significantly decreased the contribution of *Rh* to *Rs* compared with that of the control and precipitation reduction treatments, and precipitation reduction only significantly decreased the contribution of *Rh* to *Rs* compared with that of the control treatment in 2017. The results suggest that the N addition played a more important role than precipitation reduction in changing the contribution of *Rh* and *Ra* to *Rs*. Moreover, the N addition and precipitation reduction significantly increased the Q_{10} value of the *Rs* and *Rh*, suggesting that the N addition and precipitation reduction may alter the response of soil C emission to global climate warming to a certain degree. However, the study highlights the crucial importance of the impacts of N addition, precipitation reduction, and their interaction on *Rs* and its components and could improve predictions of the future states of the soil C cycle in response to global climate change.

1. Introduction

As one of the largest fluxes in the global terrestrial carbon (C) cycle, soil respiration (*Rs*) plays a vitally important role in regulating soil C pool and atmospheric CO_2 concentration (Bond-Lamberty and Thompson, 2010). The *Rs* includes heterotrophic respiration (*Rh*) and autotrophic respiration (*Ra*). The *Ra* is soil C efflux from live plant roots (mainly live fine root) and their symbionts, whereas the *Rh* is soil C efflux from the decomposition of soil organic matter and litter (Schindlbacher et al., 2009). Therefore, as combination of *Rh* and *Ra*, *Rs* is influenced by a complex array of biological and non-biological factors, including soil nitrogen (N) availability, soil water availability, microbial biomass, and fine root biomass, etc. (Zhang et al., 2014; Wang et al., 2017). In recent decades, despite *Rs* having been studied extensively, uncertainties on predicting soil CO_2 efflux still arise, mainly occurring because the rate of *Rs* is affected by rapid ongoing

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climate change (e.g., N deposition, altered precipitation and climate warming), and environmental changes caused by global climate change have a different effect on the *R*h and *R*a (Laganière et al., 2012; Cheng et al., 2015; Zhou et al., 2016; Wang et al., 2017). Thus, comprehending the controlling mechanisms of *R*s, *R*a and *R*h are important to accurately predict soil CO_2 cycling under global climate change (Zhou et al., 2014).

In recents decades, anthropogenic reactive N deposition has substantially increased in terrestrial ecosystems (IPCC, 2013; Liu et al., 2013; Penuelas et al., 2013). Due to widespread N limitation in terrestrial ecosystems (Elser et al., 2007), an increase in N deposition from human activities can strongly alter the soil N availability, which inevitably affects the *R*s and its components and then the soil C pool (Zhou et al., 2014). Numerous field manipulation experiments and several global meta-analysis studies have been conducted to examine the impacts of N deposition on *R*s, *R*a and *R*h (Zhang et al., 2014; Zhou et al., 2014; Chen et al., 2016; Zhou et al., 2016; Chen et al., 2017). Although N is one of the most important factors limiting terrestrial productivity (Xia and Wan, 2008), impacts of N addition on *R*s are sometimes inconsistent with studies having reported either increases, decreases, or no change in efflux (Yan et al., 2010; Zhang et al., 2014; Wang et al., 2017). The reason for the different results may be that (1) previous studies have generally regarded *R*s as a single variable, without considering the different effects of the N addition on the *R*h and *R*a (Zhou et al., 2016) and (2) impacts of N addition on *R*s are sometimes inconsistent due to different soil moisture conditions, soil temperature, the amount of N addition and background value of soil N (Yan et al., 2010; Gao et al., 2014). Although some studies have evaluated distinct responses of *R*h and *R*a to N addition (Janssens et al., 2010; Wang et al., 2017), knowledge of the mechanisms underlying the responses of *R*s to N addition is still limited. However, distinguishing the response of two components (*R*a and *R*h) to N addition will provide important insights into the impact of N deposition on the global soil C dynamic.

Furthermore, previous studies reported that change in precipitation pattern, always coupled with an increase in N deposition, can affect belowground biochemical processes, resulting in a change in *R*s and its components (Yan et al., 2010; Zhou et al., 2016). With the expected changes in intensity and frequency of precipitation as a result of the current climate change scenario, precipitation will decrease in some areas (IPCC, 2013). In general, single-factor manipulation experiments of precipitation reduction may substantially stimulate (Petrakis et al., 2017), significantly inhibit (Liu et al., 2016), or have no effect (Zhou et al., 2016) on the *R*s. The impacts of precipitation reduction on the *R*s were different, depending on the natural precipitation intensity and level of the precipitation reduction. Moreover, these inconsistent results may also result from the different impacts of precipitation reduction on *R*h and *R*a. To accurately evaluate the impact of precipitation reduction on *R*s and its components, an understanding of whether the responses of *R*h and *R*a to precipitation reduction can be distinguished is highly needed. However, climate change often includes simultaneous changes in multiple environmental factors (e.g., warming, N deposition and changes of precipitation pattern, etc.), which may interactively affect the *R*s, *R*h and *R*a (Zhou et al., 2016). Although many single-factor manipulation experiments were established to determine the effect of N addition or precipitation reduction on *R*s and its components (Petrakis et al., 2017; Wang et al., 2017), those experiments may be inadequate to fully understand the tendency of *R*s and its components under simultaneous changes in atmospheric N deposition and precipitation pattern (Zhou et al., 2016).

On the basis of the abovementioned background, to investigate the impacts of precipitation reduction, N addition and their interaction on *R*s, *R*h and *R*a, we conducted an 8-year field manipulation experiment in a temperate forest ecosystem in northern China. The main aims of this study were: (1) to assess the impacts of N addition and precipitation reduction on *R*s and its components; (2) to assess whether the contributions of *R*a and *R*h to *R*s change under N addition and precipitation reduction; (3) to investigate the impacts of precipitation reduction and N addition on the Q_{10} of the *R*s and *R*h; and (4) and to examine the interaction effects of precipitation reduction and N addition on the *R*s and its components. Previous studies suggested that *R*s had a positive response to N addition and a negative response to precipitation reduction, whereas *R*h had a similar negative response to N addition and precipitation reduction (Janssens et al., 2010; Liu et al., 2016; Zhou et al., 2016). Therefore, we hypothesized that (1) N addition would enhance *R*s because the increasing N availability may increase microbial biomass and fine root biomass, contrary to precipitation reduction; (2) N addition and precipitation reduction would decrease *R*h but increase *R*a, which may cause by stronger nutrient competition in root system than that in microorganisms; and (3) N addition, coupled with precipitation reduction, would also change the *R*s, *R*a and *R*h, and the contributions of *R*a and *R*h to *R*s.

2. Materials and methods

2.1. Site description

The experimental fields are located in an old broad-leaved Korean pine mixed forest (˜200 years old) in Changbai Mountain Natural Reserve, northeastern China (42°24′N, 128°05′E). The average annual temperature is 3.6 °C; average growing season temperature is 15 °C (from 1982 to 2003, Zheng et al., 2017); the highest monthly mean temperature is 21.5 °C, occurring in August; and the lowest monthly mean temperature is -17.3 °C, occurring in January. The average annual precipitation is approximately 740 mm. The soil in the study sites was developed from volcanic ash and is classified as a Eutric cambisol (FAO classification). The dominant tree species are *Tilia amurensis*, *Pinus koraiensis* and *Quercus mongolica*. The average canopy height for these three species is 26 m. The main shrub species are *Deutzia scabra*, *Corylus mandshurica*, *Lonicera japonica*, *Euonymus alatus*, *Philadelphus schrenkii*, and the main herbaceous species are *Filipendula palmate*, *Adonis vernalis*, *Cyperus microiria*, *Brachybotrys paridiformis*, *A. cathayensis*, and *Anemone raddeana*.

2.2. Experimental design and treatments

The amount of precipitation has decreased in North China over the last 50 years (Wang et al., 2006). The amount of precipitation dropped to 550 mm in the drought years (e.g., 1985, 1997, 1999, 2001, and 2003), which is on the verge of being 30% less than the long-term mean annual precipitation of 740 mm in wet years for the last 30 years (Chinese Ecosystem Research Network, CERN). To understand the effects of precipitation reduction on *R*s, *R*a and *R*h, six 50 × 50 m plots with a > 20 m-wide buffer strip between the neighboring plots were randomly established in Changbai Mountains in September 2009. Based on the abovementioned historical data, the precipitation manipulation experiment was established with two levels of precipitation reduction (control and a 30% precipitation reduction, which is equivalent to the drought years). Each treatment had three replicates. The precipitation removal equipment was installed by using high light-transmittance (transparency 95%), polycarbonate, V-shaped, translucent panels(PC) and the polycarbonate panels covering 30% of the plot area to prevent approximately 30% of natural through-fall in the growing season, and they were removed in winter. The PC was fixed on an aluminum frame. To assess the effects of the N addition and the interaction of precipitation reduction and N addition on *R*s and its components, each of these six plots was separated into two 25 × 50 m subplots; one of the subgroups of each plot received additional N and the other did not. The mean annual bulk deposition of N was 23 kg N hm^{-2} yr^{-1} in the study area (Lü and Tian, 2007). The level of N addition was 50 kg N hm^{-2} yr^{-1}, which was approximately two times the historic N deposition rate in the study area. In each N addition subplot, ammonium nitrate

(NH_4NO_3) was weighed, mixed with 40 L of deionized water, and sprayed onto the forest floor using a backpack sprayer during the growing season (May to October). The control plots simultaneously supplied 40 L of deionized water without additional N.

2.3. Soil respiration measurement

To separate the *R*h and *R*a from the *R*s, we randomly trenched one 1 m × 1 m area to 60 cm depth (approximately the bottom of the root zone in study area) in each experimental subplot in May 2015 (12 subplots × 3 three replicates = 36 trenches total), and lined the trench with landscaping cloth to enable lateral water movement while limiting the growth of the roots into the trenched subplots. To diminish the disturbances, the trenches were backfilled according to its original soil profiles. All trenched subplots were then kept free of seedlings and herbaceous vegetation by periodic manual removal throughout the experiment.

To measure the *R*s, in each subplot, three polyvinyl chloride collars (PVC, 20 cm in diameter and 6 cm in height) were installed outside of each trench, and three more were installed inside of each trench in each subplot. PVC collars were inserted 2–3 cm deep into the soil. To minimize the effect of dead roots caused by trenching, the *R*s was measured 1 year after trenching. During the growing season, the *R*s was measured twice per month from May to October of 2016 and from May to October of 2017 by using the Li-8100 (Li-Cor Inc., USA), respectively. The interval between the two measurements was one week, and the average value of the two times represented the monthly *R*s. Each measurement of each collar was repeated 3 times to produce a collar's mean *R*s rate. During each *R*s measurement, the soil temperature at 5 cm depth and the soil volumetric water content at the 5 cm depth were monitored simultaneously with the measurement of *R*s by using a Li-Cor thermocouple (Omega Engineering Inc. USA) and soil moisture probes (Deltat Devices Ltd., Cambridge, England) connected to Li-8100. Soil CO_2 efflux rates measured in the trenched subplots were represented as the *R*h, whereas the difference between the soil CO_2 efflux rates in the untrenched and trenched plots was represented as the *R*a. The precipitation and daily soil temperature at the 5 cm depth (T_5) were retrieved from Chinese Ecosystem Research Net (CERN) data during the study periods (2016–2017).

2.4. Soil sampling and analysis

The soil samples were collected in September of 2016 and 2017, respectively. Six soil cores from each untrenched plot were randomly collected from each subplot at a depth of 0–10 cm using a 5 cm diameter stainless steel auger for the measurement of fine root biomass (diameter ≤2 mm) in September of 2016 and 2017. All roots were rinsed with water, dried in an oven at 75 °C, and weighed to determine fine root biomass. To determine the effect of N addition and precipitation reduction on soil microbial biomass and soil properties, six soil cores of each subplot were randomly taken from the top layer (0–10 cm) by using a handheld auger (diameter 5 cm). All soil cores of each subplot were combined, and the visible extraneous materials (such as roots, stones, etc.) were removed from each soil sample by hand. Then, each composite soil sample was divided into two sub-samples: the first one was air-dried and then was sieved (2 mm) for the analysis of basic soil properties, and the second one was transported to the laboratory in a 4 °C cooler for the later measurement of soil microbial biomass. The soil pH was measured using a pH meter (Sartorius PB-10, Gottingen, Germany) with a 1:2.5 (soil: water, weight/volume) ratio of soil to water. The soil total C and N were measured by using a Multi N/C 3100 Analyzer (multi N/C 3100, Analytik Jena AG, Germany). The soil dissolved total C (DTC) and dissolved total N (DTN) were extracted from 10 g soil using 2 mol/L KCl extraction procedures and were measured using a Multi N/C 3100 Analyzer. The soil total phosphorus (P) was measured using the molybdenum antimony anti-colorimetric method. The soil microbial biomass C (MBC) was estimated with the chloroform-fumigation extraction method (Brookes et al., 1985). MBC was extracted from 10 g soil using 0.5 mol/L K_2SO_4 and determined by using a Multi N/C 3100 Analyzer from fumigated and unfumigated soils. The conversion factor (kEC) of 0.45 was used for calculating the MBC values (Brookes et al., 1985).

2.5. Statistical analyses

We used the bivariate model to analyze the relationship between the *R*s and the soil temperature and moisture (Eq. (1)).

$$R = ae^{bT}W^{c} \quad (1)$$

where R represents the rate of soil respiration (*R*s or *R*h, μmol m^{-2} s^{-1}); T represents the soil temperature at 5 cm depth (°C); W (%) represents soil volumetric moisture at 5 cm depth; and a, b, and c represent model parameters.

Temperature sensitivity (Q_{10}) was calculated using Eq. (2).

$$Q_{10} = e^{10b} \quad (2)$$

The Q_{10} was separately calculated at each treatment, and the diff ;erences among the Q_{10} of the different treatments were statistically tested using analysis of variance (ANOVA).

A repeated-measures ANOVA was performed to look for significant differences in *R*s, *R*h, *R*a, and soil moisture and soil temperature among different treatments during the measurement period. A general linear model with Tukey's HSD was used to examine the differences among the different treatments in the microbial biomass, soil chemical parameters, fine root biomass, and the averages of the *R*s, *R*h, and *R*a. Linear regression models were used to further explore the relationship among *R*s, *R*h, *R*a, soil chemical variables, microbial biomass and fine root biomass. All statistical analyses were performed using the SPSS software version 17.0 (SPSS, IBM, USA).

3. Results

3.1. Precipitation patterns and soil properties

During the two growing seasons, soil temperature at 5 cm soil depth showed clear seasonal patterns, with the highest temperature in the August and the lowest in the October (Fig. 1A). Soil temperature ranged from 1.23 to 22.67 °C during the study period. The mean soil temperature was 13.67 °C and 14.48 °C in 2016 and 2017, respectively. The maximum soil temperature was 22.67 °C in the 2017 wes higher than that for 2016 (20.76 °C).

Precipitation during the growing season (May to October) was 755 mm in 2016, and 590 in 2017 (Fig. 1A). Precipitation in 2017 decreased by 21.82% compared with that in 2016. If the non-growing season included, the annual precipitation in 2016 was higher than the mean of wet year (740 mm) and the annual precipitation in 2017 was possible similar to long-time average annual precipitation (740 mm). Precipitation in 2016 was the highest (213 mm) in August and the lowest (42 mm) in October, and roughly evenly distributed in the other months. Furthermore, more than 65% of the seasonal precipitation occurred in July and August, which resulted in a more uneven distribution of precipitation during the growing season.

Soil moisture at the 5 cm soil depth showed a close relationship with precipitation fluctuations during the two growing seasons (Fig. 1B). During the measurement periods, soil moisture was significantly higher in the control treatments than that in the precipitation reduction treatments. However, the decrease was dependent on the intensity of the precipitation and was relatively higher in the months of high precipitation (Fig. 1B). When precipitation was higher, the difference in the soil moisture between precipitation reduction and the control was bigger (Fig. 1B).

During the measurement period, the N addition significantly

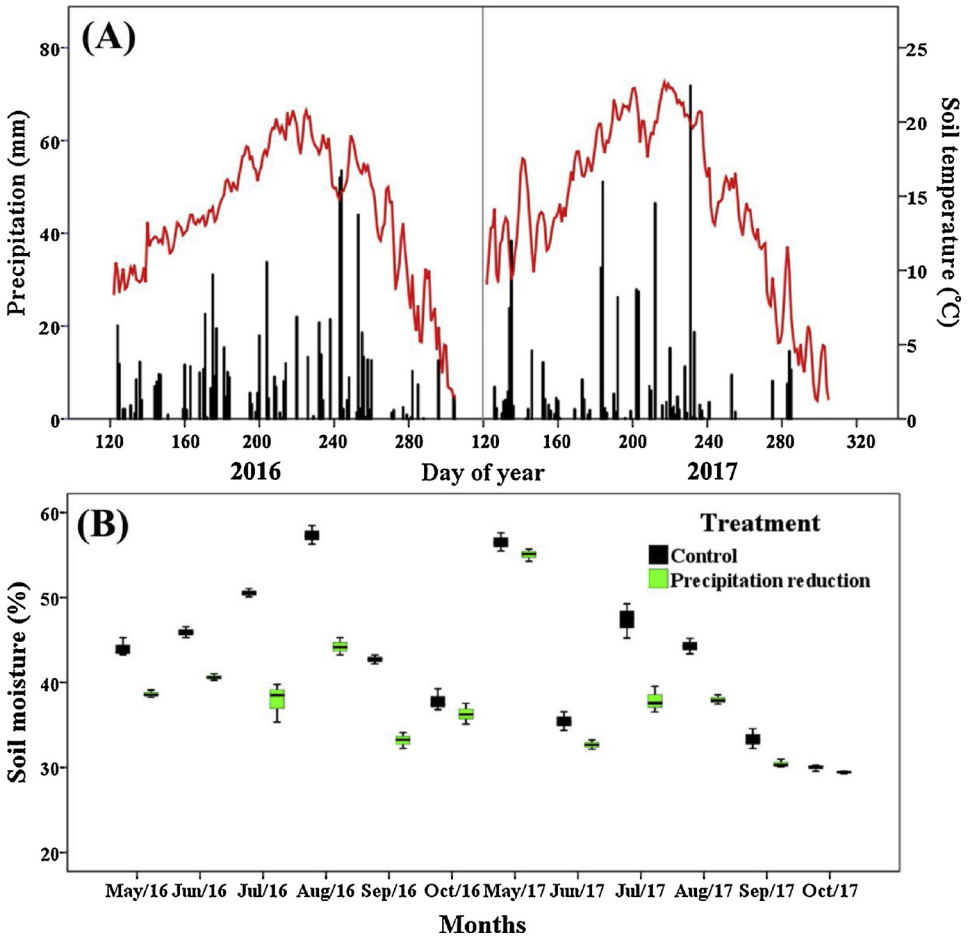

Fig. 1. The precipitation and daily soil temperature at the 5 cm depth (T_5) (these data comes from Chinese Ecosystem Research Net (CERN) data) during the measurement periods in 2016–2017 (A). soil moisture (%) at the 5 cm depth (W_5, %) under control and precipitation reduction treatments in different months of 2016–2017 (mean value ± standard error). (B).

Table 1
Basic physicochemical characteristics of the soil (0–10 cm) from the treatment plots in 2016 and 2017 (mean ± SE).

		Total C	Total N	Total P	pH	DTC	DTN
2016	Control	88.52 ± 4.33a	5.53 ± 0.40a	1.66 ± 0.09a	4.73 ± 0.04a	0.62 ± 0.04b	0.05 ± 0.01b
	+N	95.90 ± 14.16a	5.96 ± 0.36a	1.64 ± 0.10a	4.52 ± 0.12b	0.72 ± 0.03a	0.07 ± 0.02a
	-P	94.03 ± 8.01a	6.06 ± 1.32a	1.62 ± 0.11a	4.86 ± 0.09a	0.68 ± 0.09a	0.06 ± 0.01b
	+N-P	83.07 ± 4.57a	5.86 ± 0.40a	1.68 ± 0.05a	4.64 ± 0.04b	0.61 ± 0.03b	0.05 ± 0.00b
2017	Control	85.89 ± 6.75a	5.63 ± 0.15a	1.60 ± 0.11b	5.15 ± 0.08a	0.52 ± 0.02b	0.05 ± 0.02b
	+N	93.98 ± 7.18a	6.02 ± 0.27a	1.58 ± 0.16b	4.87 ± 0.05b	0.61 ± 0.04a	0.08 ± 0.02a
	-P	93.01 ± 5.67a	6.12 ± 0.39a	1.70 ± 0.16a	5.14 ± 0.03a	0.61 ± 0.05a	0.06 ± 0.01b
	+N-P	83.65 ± 5.66a	5.93 ± 0.26a	1.71 ± 0.16a	4.93 ± 0.09b	0.57 ± 0.13b	0.06 ± 0.02b

–P represents the precipitation reduction treatments; +N represents the N addition treatments; +N-P represents the N addition and precipitation reduction treatments. Total C represents the soil total C; Total N represents the soil total N; Total P represents the soil total P; DTC represents the soil dissolved total C; DTN represents the soil dissolved total N.

decreased the pH value and significantly increased the DTN and DTC content compared with that of the control but did not significantly affect the total C and total N content (Table 1). The reduction in the precipitation significantly increased the DTC and the total P content compared with that of the control but did not significantly affect the total C, total N, pH value and DTN (Table 1). Furthermore, the N addition and precipitation reduction significantly increased the microbial biomass in 2016 and 2017. Under N addition, the fine root biomass significantly increased in 2016 and 2017, but precipitation reduction only significantly increased the fine root biomass in 2016. The interaction of N addition and precipitation reduction significantly increased the microbial biomass in 2016 and significantly decreased the fine root biomass in 2017 (Fig. 2).

3.2. Soil respiration and its components

The temporal dynamics of the *R*s, *R*h, and *R*a were consistent with the seasonal pattern of soil temperature in both years, with a peak value during July-August and low rate at end of the growing season (October), and the difference between the values in the different months was significant (Fig. 3). At the beginning of the growing season (based on phenology, leaf-unfolding dates, Jeong et al., 2011), the *R*h was always significantly higher than the *R*a. When averaged across both growing season, rates of the *R*s, *R*h, and *R*a were 2.68, 1.76 and 0.92 μmol CO_2 m^{-2} s^{-1}, respectively. *R*s and *R*a in the 2016 was significantly lower than those in the 2017 ($p < 0.05$), which may be mainly due to the interannual change in the precipitation pattern affecting the fine root biomass.

Nitrogen addition and precipitation reduction did not alter the

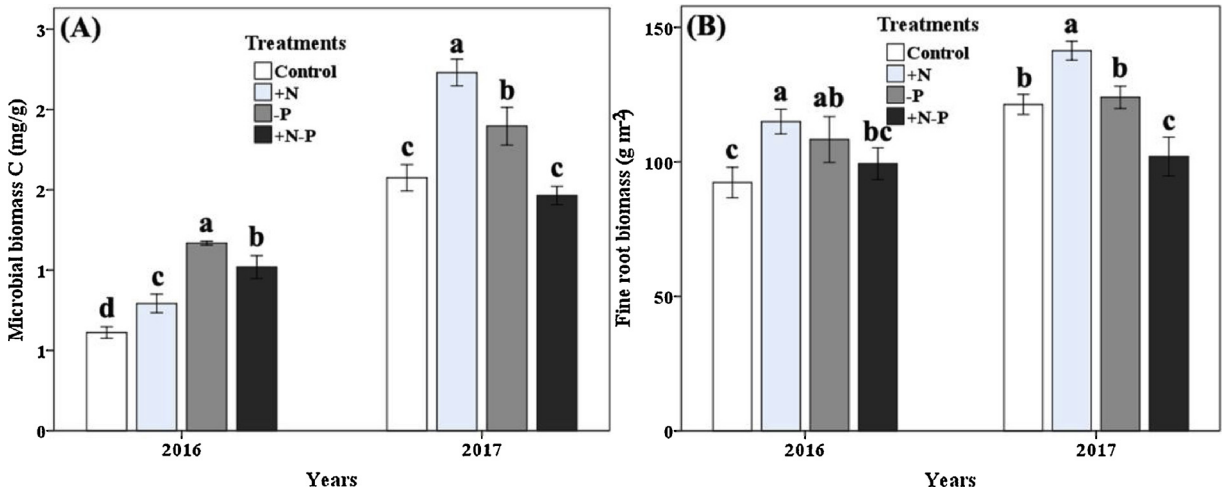

Fig. 2. Comparison of mean fine root biomass (A) and microbial biomass C (MBC) (B) among different treatments in 2016 and 2017. -P represents the precipitation reduction treatments; +N represents the N addition treatments; +N-P represents the N addition and the precipitation reduction treatments. Significant differences ($P < 0.05$) among the different treatments are indicated by different letters. Error bars represent SD.

seasonal dynamics of the *R*s, *R*h and *R*a (Fig. 3). During the measurement period, the mean annual *R*s, *R*h and *R*a had a significant positive response to precipitation reduction and N addition, although the responses of the *R*s, *R*h and *R*a to precipitation reduction and N addition were not completely consistent in different months. In 2016, the N addition significantly increased the *R*s, *R*h and *R*a by 33%, 13% and 94%, respectively, compared with those of the control. In 2017, the N addition significantly increased the *R*s, *R*h and *R*a by 59%, 62% and 96%, respectively. These findings indicated that the effects of the N addition on *R*s, *R*h and *R*a in 2017 were greater than those in 2016. The precipitation reduction in 2016 significantly increased the *R*s, *R*h and *R*a by 25%, 33% and 75%, respectively, compared with those of the control. The precipitation reduction in 2017 significantly increased the *R*s, *R*h and *R*a by 11%, 15% and 31%, respectively, compared with those of the control. These results indicate that the effects of the precipitation reduction on the *R*s, *R*h and *R*a in 2017 were smaller than those in 2016. The interaction of the N addition and precipitation reduction significantly increased the *R*s, *R*h and *R*a in 2016, but did not significantly affect the *R*s and *R*h in 2017. Furthermore, the *R*a had a significant negative response to the interaction in 2017.

The contributions of the *R*h and *R*a to *R*s were different under the different treatments (Table 2). In summary, the contribution of the *R*h to *R*s was significantly higher (51.8–85.5%) than that of the *R*a in all treatments ($p < 0.05$). The contribution of the *R*h to *R*s under the N addition significantly decreased on average across the two growing seasons, whereas the precipitation reduction significantly decreased the contribution of the *R*h to the *R*s in 2017, but did not show a significant effect in 2016, suggesting that the effect of precipitation reduction on the contributions of *R*a and *R*h to *R*s may be regulated by climatic conditions in different years. For N addition, the contribution of the increased *R*h and *R*a to the enhancement of *R*s was 28.0% and 72.0% in 2016, and 52.4% and 47.6 in 2017, respectively (Fig. 4), indicating that the contribution of the increased *R*h to the enhancement in *R*s varied among years. For precipitation reduction, the contribution of the increased *R*h and *R*a to the enhancement of *R*s was 54.7% and 45.3.0% in 2016, and 41.3% and 58.7% in 2017, respectively (Fig. 4). For their interaction, the contribution of the increased *R*h to the enhancement of *R*s was 45.2% and 54.8% in 2016, respectively, and the contribution of the decreased *R*h to the decline in *R*s was 22.1% and 77.9% in 2017, respectively.

3.3. Soil respiration and its components response to soil environmental factors

The relationships of the *R*h, *R*a and *R*s with the major biotic and abiotic factors are given in Table 3. The *R*h, *R*a and *R*s were significantly positively correlated with fine root biomass. Microbial biomass C was significantly positively correlated with *R*h and *R*s, but not with *R*a. The DTC was positively correlated with the *R*h and *R*a but not with *R*s. Soil total P was significantly negatively correlated with *R*s and *R*a, but not with *R*h.

A bivariate exponential function with soil moisture and temperature was used to explain the *R*s and *R*h in Table 4. The soil moisture and temperature explained 66–84% and 36–78% of the variations in *R*s and *R*h, respectively. The soil moisture and temperature explained more variations in *R*s in the N addition and the control treatments than those in other treatments and explained more variations in the *R*h in the N addition and precipitation reduction treatments than those in the other treatments. During the measurement period, the fitted Q_{10} values of the *R*s ranged from 1.83 to 2.23, and the Q_{10} value of *R*h ranged from 2.02 to 2.47. The Q_{10} values of *R*s in precipitation reduction and combined N addition and precipitation reduction were significantly higher compared with those of the control, and the Q_{10} values of *R*h in N addition and precipitation reduction were significantly higher compared with those of the control (Table 4).

4. Discussion

In the study, the results showed that precipitation reduction and N addition significantly increased the soil CO_2 flux, which was consistent with the previous studies on the effect of N addition and precipitation reduction on soil CO_2 flux (Zhang et al., 2014; Zhou et al., 2016; Meyer et al., 2018). However, the soil CO_2 flux consists of *R*a and *R*h, and the impacts of the N addition and precipitation reduction on the *R*a and *R*h determined the direction of the *R*s response.

4.1. Effects of N addition on soil respiration and its components

The factorial impacts on *R*a and *R*h are caused by the direct and indirect impacts of N on tradeoffs among the components of plant gross primary production and substrate concentrations (Chen et al., 2013). Therefore, N addition can affect *R*a through several processes correlated with changes in the biological and non-biological factors (Wang et al., 2015). First, the impacts of N addition on biomass allocation of plant and nutrient concentrations may help further explain how the N

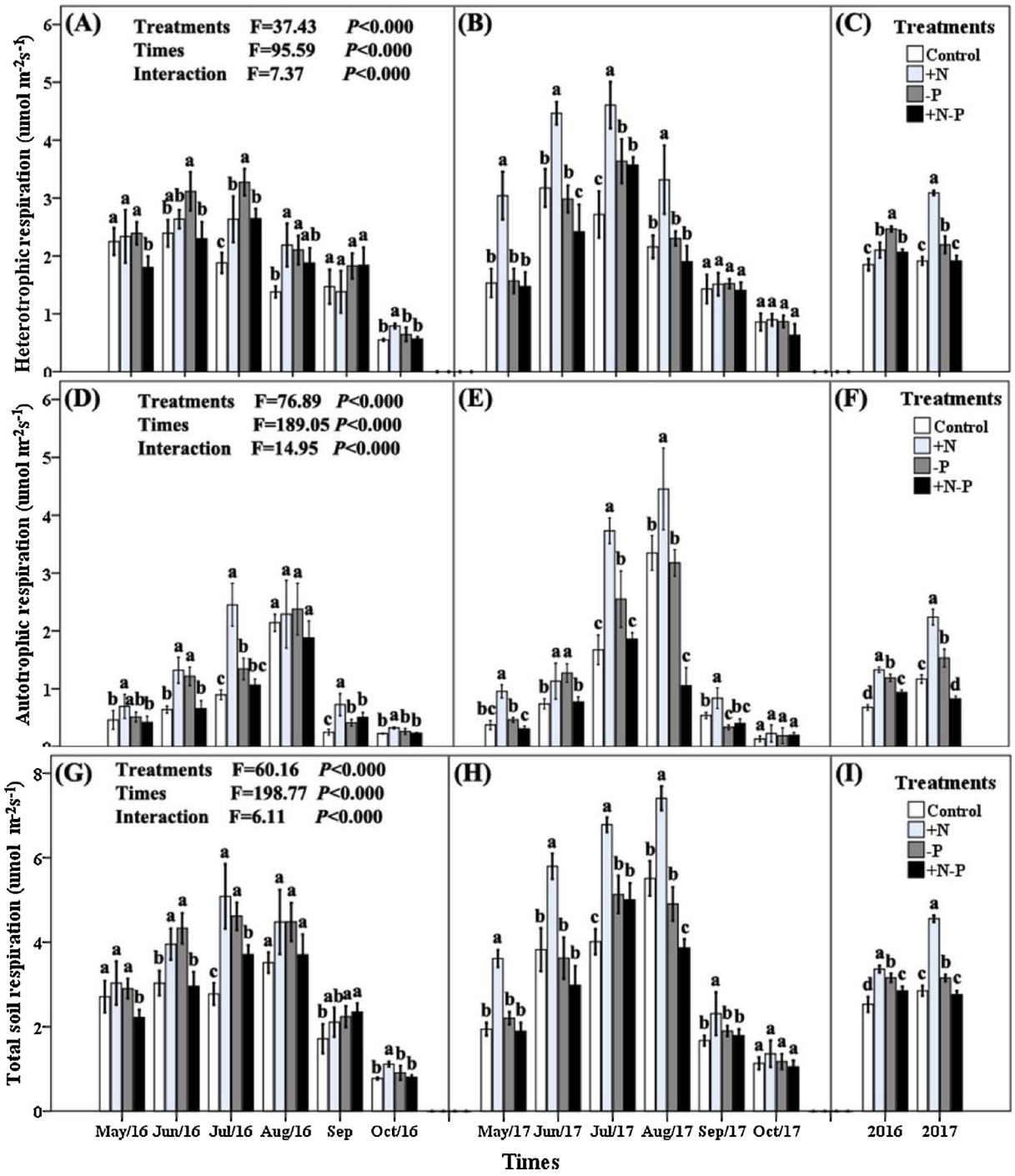

Fig. 3. Temporal changes in total soil (G, H), heterotrophic (A, B), and autotrophic (D, E) respiration, and their mean value (C, F, I) among the different treatments during the measurement periods in the growth season of 2016 and 2017. The error bars are standard errors. Different lowercase letters represent statistical significances among treatments in same month. -P represents the precipitation reduction treatments; +N represents the N addition treatments; +N-P represents the N addition and the precipitation reduction treatments.

addition affected *Ra* in the soil under variable environmental conditions. It was usually expected that N addition alleviated soil N limitation, which may lead to a reduction in the allocation of assimilates belowground and to a decrease in the biomass of fine roots (Sun et al., 2014), consistent with the theory of optimal allocation. However, an increase of soil N availability can lead to other nutrient limitations (e.g., P) (Li et al., 2015), in part because the availability of P has not increased concurrently (Huang et al., 2016). In addition, Liebig's law of the minimum suggests that, in systems already limited by P availability (Chapin, 1980), we might expect that enhanced soil N availability may have little effect on plant functioning, an emerging idea about colimitation which suggests that limitations on ecosystem productivity probably result from a single resource at a time (Braun et al., 2010; Farrior et al., 2013). Plants are likely to adjust biomass allocation in response to soil nutrient availability, increasing allocation to some structures that acquire a limited resource (Valliere and Allen, 2016). Thus, due to the N addition and increased soil P deficiency (may also other nutrients), the plant had to acquire P from previously unavailable pools for their growth, which lead to an increase in the fine root biomass and resulted in the rise in *Ra* (Fig. 3); the significantly positive

Table 2
Mean values of the contribution of heterotrophic respiration (*Rh*) to total soil respiration (*Rs*) (%) in different months (mean ± SE).

		May	June	July	August	September	October	Average
2016	Control	81.2 ± 2.2a	78.9 ± 2.3a	67.7 ± 2.6a	41.2 ± 1.5b	71.2 ± 2.3a	85.4 ± 1.8a	70.9 ± 2.1a
	+N	77.3 ± 1.8b	66.9 ± 3.3b	51.8 ± 2.6b	48.9 ± 2.0a	59.8 ± 1.7b	67.6 ± 1.5c	62.1 ± 2.2b
	-P	81.9 ± 2.7a	72.4 ± 4.4b	72.2 ± 3.4a	48.4 ± 1.5a	71.0 ± 1.9a	83.4 ± 2.3a	71.6 ± 2.7a
	+N-P	80.7 ± 2.9a	78.3 ± 2.7a	71.8 ± 4.0a	51.4 ± 2.9a	68.4 ± 2.0a	78.6 ± 1.6b	71.5 ± 2.9a
2017	Control	83.0 ± 2.3a	78.9 ± 3.9a	67.7 ± 3.4a	46.8 ± 2.1b	75.9 ± 2.6a	85.5 ± 4.5a	73.5 ± 3.1a
	+N	78.1 ± 4.6a	68.8 ± 1.4b	51.8 ± 2.4b	44.9 ± 0.9b	63.1 ± 1.7b	75.5 ± 2.8b	64.2 ± 2.3c
	-P	82.4 ± 3.8a	71.2 ± 2.1b	55.9 ± 1.8b	49.9 ± 1.2a	66.8 ± 2.4b	81.6 ± 4.2a	66.9 ± 2.6b
	+N-P	81.1 ± 2.6a	77.7 ± 1.2a	71.3 ± 4.6a	49.2 ± 0.8a	61.9 ± 4.6b	78.4 ± 3.1a	69.9 ± 2.8ab

-P represents the precipitation reduction treatments; +N represents the N addition treatments; +N-P represents the N addition and precipitation reduction treatments. Different letters in the same year among treatments indicate significant differences ($p < 0.05$). Data were mean ± SE.

relationship between *Ra* and fine root biomass also supported this conclusion (Table 3). The N addition stimulated *Ra* by increasing the fine root biomass, which has been shown to produce a direct positive impact on rhizosphere respiration (Meyer et al., 2018). Whereas there was a significant negative correlation between *Ra* and P, which didn't mean that soil P is sufficient or too high because majority of phosphorus is occluded and is not available for plant uptake in acidic soil. Significant negative correlation between *Rs* or *Ra* and P may also suggest that plants may absorb available P from the soil and then return to the soil in the form of litter organic P, which could aggravates the limitation of available P in the soil. However, in this study, we did not measure the concentration of available P, and the change of available P may need to pay much attention in future work.

The increase in *Rh* after N addition was consistent with the previous studies (Zhang et al., 2014; Meyer et al., 2018). *Rh* is derived from the decomposition of litter or soil organic matter (Janssens et al., 2010). Availability of soil N can affect belowground microbial biomass and activity, with potential consequences for *Rh* in N-limited ecosystems (Gardenas et al., 2011). The N addition significantly increased the soil N availability, which often resulted from mitigating the impacts of N limitation on the soil microbes, and thereby increased the microbial activity and biomass (Zhang et al., 2014). In our study, the increase in soil microbial biomass caused *Rh* enhancement following the N addition (Fig. 2). Furthermore, the increase in fine root biomass increased the input of soluble organic compounds (e.g., root exudates) exuded by fine root and mycorrhizal hyphae to the soil (Högberg and Högberg, 2002), which might lead to an increase in the *Rh* after the N addition. In this experiment, the effect of root exudates was not determined, as the absence of roots during the measurement of *Rh* excludes the supply of root exudates that were respired by soil microbes, and the *Rh* measured in the root-free plots might be an underestimate of actual *Rh* (Zhang et al., 2014). Moreover, the trenching method of root exclusion also eliminates the competition of root and microbes for nutrients (e.g., soil P), which may relatively enhance the availability of P in soils for the soil microbes (substrate competition theory).Increases in substrate concentrations, especially the limiting factor concentration (e.g., availability of N and P), are well known to lead to an increase in microbial biomass and activity, resulting in an increase in *Rh* (De Nobili et al., 2001). By contrast, some previous studies also reported a different result, where the *Rh* might be inhibited by an increase in soil N availability (Janssens et al., 2010; Wang et al., 2017). The different N

Table 3
The correlation coefficients between soil respiration and soil chemical properties and fine root biomass.

	Total C	Total N	Total P	pH	DTC	DTN	MBC	FRM
Rs	0.15	0.32	−0.60*	−0.10	0.26	0.34	0.45*	0.43*
Rh	0.26	0.29	−0.10	0.39	0.46*	0.40	0.67**	0.62**
Ra	0.27	0.43	−0.55*	−0.24	0.52*	0.39	0.35	0.82**

Rs represents the total soil respiration; *Rh* represents the heterotrophic respiration; *Ra* represents the autotrophic respiration; Total C represents the soil total C; Total N represents the soil total N; Total P represents the soil total P; DTC represents the soil dissolved total C; DTN represents the soil dissolved total N; MBC represents the microbial biomass carbon; FRM represents the fine root biomass.

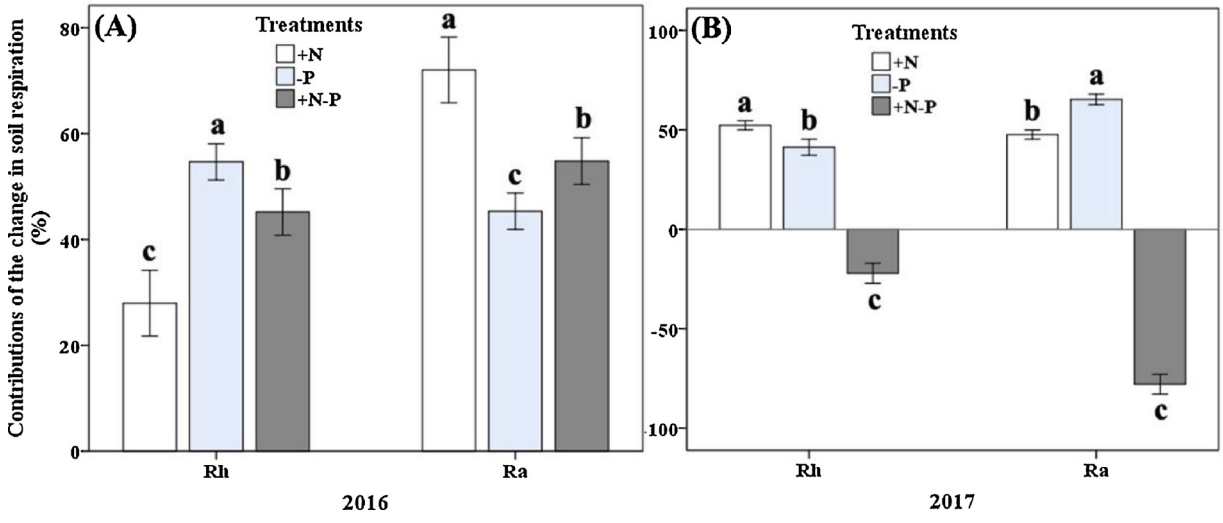

Fig. 4. The contributions of the increase in autotrophic (*Ra*) and heterotrophic (*Rh*) respiration to the rise in total soil respiration induced by different treatments in 2016 and 2017. Positive values represent increase, negative values represent decrease. -P represents the precipitation reduction treatments; +N represents the N addition treatments; +N-P represents the N addition and the precipitation reduction treatments. Significant differences ($P < 0.05$) among different treatments are indicated by different letters. Error bars represent SD.

Table 4
Parameter estimates of models for *Rs* and *R*h as a function of soil temperature (T) and moisture (W) in the 0–5 cm soil from May 2016 to October 2017 in different treatments (mean ± SE).

	a	b	c	R^2	*P*	Q_{10}
$Rs = ae^{bt}w^c$						
Control	0.89 ± 0.06	0.06 ± 0.01***	0.37 ± 0.08***	0.80	0.000	1.83 ± 0.11b
+N	1.38 ± 0.15*	0.07 ± 0.01***	0.61 ± 0.09***	0.84	0.000	2.02 ± 0.20ab
-P	0.63 ± 0.10***	0.08 ± 0.00***	0.07 ± 0.02**	0.68	0.000	2.23 ± 0.05a
+N-P	0.56 ± 0.12***	0.08 ± 0.01***	0.07 ± 0.04	0.66	0.000	2.23 ± 0.22a
$Rh = ae^{bt}w^c$						
Control	0.47 ± 0.07**	0.07 ± 0.01***	0.04 ± 0.09	0.64	0.000	2.02 ± 0.07b
+N	0.46 ± 0.12*	0.09 ± 0.01***	−0.11 ± 0.14	0.72	0.000	2.47 ± 0.14a
-P	0.27 ± 0.16***	0.09 ± 0.01***	−0.47 ± 0.20	0.78	0.000	2.45 ± 0.13a
+N-P	0.37 ± 0.12	0.07 ± 0.03*	0.06 ± 0.07	0.36	0.000	2.07 ± 0.36ab

The Q_{10} value is obtained from b ($Q_{10} = e^{10b}$). a, b and c are regression coefficients. -P represents the precipitation reduction treatments; +N represents the N addition treatments; +N-P represents the N addition and the precipitation reduction treatments. Different letters in the same year among treatments indicate significant differences ($P < 0.05$). Data were mean ± SE. ANOVA: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

effects can occur in response to biome types, environmental conditions, and experimental methods (Moscatelli et al., 2008; Zhou et al., 2014).

4.2. Effects of precipitation reduction on soil respiration and its components

Soil moisture affects *R*a and *R*h directly through the physiological processes of microbes and roots, and indirectly via diffusion of O_2 and substrates (Cheng et al., 2015; Aaltonen et al., 2017). However, lots of precipitation reduction treatments have suggested that the *Rs* decreases with reductions in soil moisture (Suseela et al., 2012; Jiang et al., 2013). In our study, the precipitation reduction significantly increased *Rs*, *R*a and *R*h in the rainy season (e.g. August), but had no significant effect on soil respiration in the dry season (e.g. October), which was consistent with a previous study (Zhang et al., 2015; Aaltonen et al., 2017). The different results may be due to the intensity of annual precipitation and different duration and intensity of the precipitation reduction. For example, under the severe and longer-lasting drought, *Rs*, *R*a and *R*h have been commonly observed to decline (Suseela et al., 2012; Jiang et al., 2013; Hasibeder et al., 2015). Whereas under a wet years, as in our study, precipitation reduction may be beneficial to improving soil oxygen availability, which may lead to better plant growth and afford more C substrate to root/rhizosphere respiration (Brunner et al., 2015; Aaltonen et al., 2017). Given the tight linkage between plant C allocation strategy and *R*a, precipitation reduction can alter the allocation of assimilates to roots, as well as to the respiration of the plant roots and their symbionts (Poorter et al., 2012). In this study, the fine root biomass under precipitation reduction treatments was significantly higher than that in the control treatments (Fig. 2), resulting in the increase of *R*a (Fig. 3), and the positive relationship between the *R*a and the fine root biomass also supported the conclusion. In general, the precipitation reduction in a wet years can modify the ability of the trees to allocate new assimilates to roots, suggesting precipitation reduction may increase root growth by increasing soil oxygen availability in precipitation-rich years.

Different from *R*a, the enhancement of *R*h could be due to the increase in microbial biomass, as our results have shown that the MBC significantly increased under precipitation reduction (Fig. 2). However, our results also show that the effect of precipitation reduction on *R*h depends on the season, with *R*h being less sensitive in the dry season to precipitation reduction and more sensitive in the rainy season to precipitation reduction (Fig. 3). At the study site, precipitation during the dry month is often < 10% of the growth season total; consequently, soil moisture in the precipitation reduction treatment would be less affected. Therefore, during the dry month (e.g., October of 2017), the *R*h did not change significantly under conditions of precipitation reduction. While, during the wet month (e.g. July of 2017), the *R*h increased significantly with precipitation reduction. We speculated that during the wet month, the soil moisture was not a limiting factor on *R*h and that soil moisture in the control plot were always higher than the soil water holding capacity in the study area, which may have reduced the air-filled porosity in the soil to low levels, thus reducing the *R*h by reducing the diffusion of CO_2 or restricting microbial activity (Silver et al., 1999; Yan et al., 2016). Under precipitation reduction conditions, the soil moisture levels were closer to the range required for optimal microbial and root activities, enabling the *R*h to increase significantly.

4.3. Interactive effects of N addition and precipitation reduction on soil respiration and its components

Although either precipitation reduction or N addition significantly increased the *Rs*, *R*a and *R*h, antagonistic non-additive effects were detected in the study. The interactive effects had a slightly positive effect on the *Rs*, *R*a and *R*h in the wet year (2016) and had a slightly negative effect on the *Rs*, *R*a and *R*h in the relative dry year (2017). These results suggest that the interactive effect of N addition and precipitation reduction on soil respiration varied with levels of soil moisture or precipitation reduction. Because the soil water availability was closely correlated to the soil N availability, the N addition can increase plant susceptibility to precipitation reduction due to an insufficient water supply resulting from N-induced changes in shoot-root ratios or mycorrhizal infection rates (Friedrich et al., 2012; Southon et al., 2012). Enhanced soil N availability may increase the fine root biomass and microbial biomass, thereby increasing the demand for soil moisture for life-sustaining activity (Southon et al., 2012). Moreover, precipitation reduction might decrease the mobility of the available soil N (Everard et al., 2010), which might weaken the effect of N addition on *Rs*, *R*a and *R*h. Increased soil water availability can enhance the responses of soil microbial communities to N addition as well (Bi et al., 2011), which indicated N addition could exert a negative impact on soil microbial activities under low water availability. Therefore, these coupling effects may be partially responsible for the observed decline of soil respiration under simultaneous precipitation reduction and N addition (non-additive effects). However, the non-additive effects may be diminished by the higher soil moisture in wet years than that in dry years. We speculated that the future increase of N deposition or fertilization might have little effect on soil respiration in a dry year. In addition, the N addition might trigger effects on soil respiration which shift from positive to negative with levels of precipitation reduction. In summary, understanding the interactions of N addition and precipitation reduction on *Rs* and its components will improve our ability to predict ecosystem C cycle responses to global climate change.

4.4. Adjustment of soil respiration and its components by N addition and precipitation reduction

Nitrogen addition and precipitation reduction affect the balance

between *R*a and *R*h as well as their contributions to *R*s by changing microbial biomass and activity and root growth and activity (Jia et al., 2010; Aaltonen et al., 2017). The N addition and precipitation reduction had a tendency to reduce the contributions of *R*h to *R*s (Table 2), possibly because the increase in the fine root biomass was more intense than the increase in microbial biomass. Moreover, the contributions of *R*h to *R*s showed clear seasonal patterns, with the highest value in May and October, and the lowest in August (Table 2). Although the seasonal dynamics of fine root biomass were not measured in the study, based on a previous study (Yan et al., 2018), we speculated that seasonal variations in fine root biomass were the main reasons for the seasonal changes in the contributions of *R*h to *R*s.

Soil temperature is also the important controlling factor on *R*s in forest ecosystems (Hanson et al., 2000) and strongly affects the seasonal variation in *R*s (Luo et al., 2016). The sensitivity temperature of *R*s (Q_{10}) is considered an important feedback determinant of the C cycle to climate in a terrestrial ecosystem (Mahecha et al., 2010). The N addition and precipitation reduction significantly increased the values of Q_{10} of *R*h and *R*s in the study, which agreed partially with Yan et al. (2010) and Guo et al. (2017). However, previous extensive studies noted that N addition and soil moisture decrease often produced negative impacts on the Q_{10} of the *R*s and *R*h (Sun et al., 2014; Lellei-Kovács et al., 2016; Luo et al., 2016; Zhang et al., 2017). This different response of the Q_{10} of the *R*s and *R*h to N addition and soil moisture reduction may be due to differences in tree species, ecosystem types, regional climates and experimental operation modes because the variation in Q_{10} is governed by biological and non-biological factors, including the substrate availability, stability of SOM, root biomass and activity, and the physiology of the soil microbe, etc. (von Lützow and Kogel-Knabner, 2009; Guo et al., 2017). The increases in the Q_{10} values of *R*s and *R*h after N addition and precipitation reduction could be due to several reasons. The first reason for the increase in Q_{10} of *R*s is that N addition and moderate precipitation reduction increase the allocation of photosynthates to the rhizosphere (Poorter et al., 2012; Meyer et al., 2018). *R*a is closely dependent on the photosynthetic substrate supply (Aaltonen et al., 2017), and increases in substrate supply to *R*a under N addition and moderate precipitation reduction maybe the reason for the increase in the Q_{10} values for *R*a and eventually for *R*s. The second reason for the increase in Q_{10} of *R*s is that the enhanced temperature sensitivity of the SOM decomposition under N addition can be well explained by the change of substrate quality characterized with C complexities (Guo et al., 2017), thereby increasing the apparent Q_{10} of the *R*h and eventually for *R*s. Another possible reason for the increase in the Q_{10} of the *R*s is that increased Q_{10} was somewhat related to the increase of soil moisture content, but the Q_{10} always declined after reaching a soil moisture threshold (Zhang et al., 2017). Possiblly, the occurrence of limited soil aeration at high precipitation might account for the decrease in *R*h after reaching a threshold value, and moderate precipitation reduction might alleviate this limitation, thereby having a positive effect on the microbial biomass and activity. These regulating effects of moderate precipitation reduction could increase the sensitivity of decomposition to temperature change, thereby increasing the apparent Q_{10} of the *R*h and eventually for the *R*s. However, our results suggest that precipitation reduction and N addition increased the temperature sensitivity of the *R*h and *R*s. Future predictions of the *R*s under global warming scenarios should consider the effect of precipitation change and N addition on temperature sensitivity of the Q_{10} of the *R*s and *R*h.

5. Conclusion

This study has demonstrated that N addition and precipitation reduction significantly increase the *R*a, *R*h and *R*s, mainly due to an increase in soil microbial biomass and root biomass or activity. The contribution of the *R*h increase to the increase in *R*s was lower than that of the *R*a increase, which might be because the increase in fine root biomass was more intense than the increase that in the microbial biomass. However, the interaction of N addition and precipitation reduction on the *R*a, *R*h and *R*s was relatively weaker than the single factor effects. These results help us understand how *R*s and its components will change under N addition and precipitation reduction, in combination or alone. Our result also suggests that the N addition and precipitation reduction regulates the responses of *R*s and its components to temperature changes in forest ecosystems. The N addition and precipitation reduction increases the Q_{10} values for both the *R*h and *R*s, highlighting the need to measure whether this phenomenon occurs across different ecosystems. Increased Q_{10} of the *R*h and *R*s under the N addition and precipitation reduction observed in our experiment suggests that the increasing N deposition due to human activities and precipitation pattern change due to climate change may raise the uncertainty in predicting the soil C losses in the scenario of global warming of terrestrial ecosystems.

Author contributions

Fei Chen, Guoyong Yan and Yajuan Xing contributed equally to the preparation and design of the entire manuscript. Qinggui Wang and Tong Liu designed the field experiment. Qinggui Wang, Guoyong Yan, Fei Chen, Tong Liu, Yajuan Xing and Junhui Zhang contributed to the preparation and design of the entire manuscript and wrote the main text. Qinggui Wang, Guoyong Yan, Fei Chen and Yajuan Xing prepared all the figures, and Junhui Zhang, Honglin Wang, Binbin Huang, Ziming Hong, Guanhua Dai and Xingbo Zheng prepared the field experiments and tables and collected the literature. All authors reviewed the manuscript.

Competing financial interests

The authors declare no competing financial interests.

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